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Citation for published version:

Ford, L & Smiseth, PT 2017, 'Asynchronous hatching in a non-avian species: a test of the hurry-up hypothesis', *Behavioral Ecology*, vol. 28, no. 3, pp. 899 - 907. <https://doi.org/10.1093/beheco/axx055>

Digital Object Identifier (DOI):

[10.1093/beheco/axx055](https://doi.org/10.1093/beheco/axx055)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Behavioral Ecology

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Asynchronous hatching in a non-avian species: a test of the hurry-up hypothesis

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10 Running title: Hurry-up hypothesis

The hurry-up hypothesis suggests that completing reproduction as soon as possible is favoured when the quantity or quality of resources used for breeding declines over time.

However, completing reproduction sooner may incur a cost if it leads to an asynchronous hatching pattern that reduces overall growth and survival of offspring.

15 Here, we present the first test of the hurry-up hypothesis in a non-avian system, the burying beetle *Nicrophorus vespilloides*, which breeds on small vertebrate carcasses. To this end, we conducted two experiments in which we provided females with an incentive to complete reproduction sooner by giving them carcasses that varied either with respect to decomposition (decomposed or fresh) or size. We recorded the delay
20 until laying, and measures of the laying pattern and fitness consequences for the offspring. As predicted, we found that larvae dispersed from the carcass earlier when females commenced oviposition sooner and that laying spread was greater when females commenced egg laying earlier. However, we found no evidence that females commenced egg laying earlier on either decomposed or larger carcasses. Our results
25 suggest that, although asynchronous hatching might emerge as a by-product of parents attempting to complete reproduction sooner, there is no evidence that females attempt to complete reproduction sooner under conditions where this would be favourable. Our results are therefore inconsistent with the hurry-up hypothesis.

30 **Key words:** egg size, environmental conditions, resource quality, resource quantity, *Nicrophorus vespilloides*, offspring fitness

INTRODUCTION

In species where parents provide food or other forms of care for their dependent offspring, parents may be under selection to respond to deteriorating environmental conditions by shortening the time from the onset of breeding until the offspring reach independence (Hussell 1972; Clark and Wilson 1981; Slagsvold 1986). This condition might be met when there is a decline in quantity or quality of food resources (Hussell 1972; Clark and Wilson 1981; Slagsvold 1986), an increase in predation rate on dependent offspring, or when climatic conditions worsen over time (Magrath 1990). The hurry-up hypothesis was proposed to explain how parent birds might respond to deteriorating environmental conditions (Hussell 1972; Clark and Wilson 1981), but the hypothesis may apply in general across animal taxa. Female birds are constrained from laying more than one egg each day, which means that it takes them several days to complete a clutch. However, because avian eggs only start developing once parents start incubating, parents control the offspring's development by simply adjusting the onset of incubation (Clark and Wilson 1981). Thus, if parent birds perceive that the peak in food supply will occur earlier than anticipated at the start of laying, they can accelerate offspring development by commencing incubation earlier instead of waiting until the clutch has been completed. However, studies on birds show that parental attempts to shorten the time until offspring independence in response to dwindling food supplies towards the end of the breeding season are also associated with greater levels of asynchronous hatching (Gibb 1950; Van Balen 1973; Nisbet and Cohen 1975; Slagsvold 1982; Slagsvold 1986; Hébert and McNeil 1999).

The hurry-up hypothesis suggests that asynchronous hatching emerges as a non-adaptive by-product due to parent birds being under selection to commence incubation before the clutch has been completed (Clark and Wilson 1981). There is good evidence that hatching asynchrony can incur substantial fitness costs because it often leads to asymmetric sibling competition with a detrimental impact on the survival

and/or growth of the last offspring to hatch (Lack 1947; Clark and Wilson 1981;
 60 Hillström and Olsson 1994; Smiseth et al. 2007). Thus, parents should be under
 selection to balance the benefits of shortening the time until the first offspring reach
 independence against the costs of producing an asynchronous hatching pattern that
 reduces the overall growth and survival of offspring. Furthermore, parents may be
 under selection to offset any undesirable fitness consequences of asymmetric sibling
 65 competition (Clark and Wilson, 1981). For example, in several birds with asynchronous
 hatching, parents produce larger eggs towards the end of the laying sequence
 (Schrantz 1943; Kendeigh et al. 1956; Holcombe 1969; Howe 1976, 1978; Bryant
 1978), thereby compensating for some of the fitness costs of asymmetric sibling
 competition given that offspring hatching mass is positively correlated with egg size
 70 (Krist 2011) and chicks hatching from heavier eggs have higher early growth (Hillström
 1999).

Although the hurry-up hypothesis was proposed for birds where parents
 incubate their eggs, it may also apply to non-avian species where eggs develop without
 incubation, provided that there is a trade-off between commencing oviposition soon
 75 after the initiation of reproduction and laying eggs synchronously. Burying beetles of
 the genus *Nicrophorus* are an ideal non-avian study system in which to test the hurry-
 up hypothesis because they exhibit hatching asynchrony similar to that of many altricial
 birds (Muller and Eggert 1990; Smiseth et al. 2006; Takata et al. 2015). These beetles
 breed on carcasses of small vertebrates, which are buried underground (Scott 1998).
 80 Females lay eggs in the surrounding soil (Pukowski 1933) and the hatching pattern is
 determined by the period of time over which the eggs are laid, termed 'laying spread'
 (Smiseth et al. 2006; Takata et al. 2015). The degree of hatching asynchrony is highly
 variable in *N. vespilloides*, ranging from 16 to 56 h with a mean of 30 h, which is
 considerable relative to the duration embryonic development (59 h) and the duration of
 85 parental food provisioning (72 h) (Smiseth et al. 2006). Burying beetles could

potentially reduce the delay until the offspring reach independence by starting to lay eggs sooner after encountering the carcass. However, because females do not mature their oocytes until they secure a carcass for breeding (Wilson and Knollenberg 1984), starting to lay very soon after encountering the carcass may be costly as females
 90 would not have time to consume enough resources to mature all of their oocytes before commencing oviposition. If this is the case, starting to lay soon after encountering the carcass may be associated with a greater laying spread and a greater level of hatching asynchrony if there is a trade-off between accelerating the maturation of some oocytes and maturing all oocytes synchronously. This may be undesirable due to increased
 95 mortality of the last hatched offspring in asynchronous broods (Smiseth et al. 2008; Takata et al. 2014; Ford and Smiseth 2016).

Here we present the results of two experiments designed to test the hurry-up hypothesis in *N. vespilloides*. We provided female beetles with an incentive to shorten the time until offspring independence in response to variation in either resource quality
 100 (i.e., carcass decomposition) or resource quantity (i.e., carcass size). We used carcass decomposition as a proxy for resource quality whilst we used carcass size as a proxy for resource quantity. We predicted that females would shorten the time until offspring independence when breeding on decomposed carcasses because the value of the carcass should decrease over time due to an increase in microbial load. Indeed,
 105 carcass decomposition has a detrimental effect on larval growth and survival (Rozen et al. 2008) and egg survival (Jacobs et al. 2014). Meanwhile, we predicted that females would start to lay sooner when breeding on larger carcasses because larger carcasses are more difficult to roll into a ball so it is more difficult to control microbial activity due to the larger surface area remaining exposed (Trumbo, 1992). Furthermore, it is more
 110 difficult for the parents to keep the carcass coated with antimicrobial secretions, which may provide an incentive to complete reproduction sooner on larger carcasses, before decomposition of the carcass becomes detrimental to the larvae. In addition, larger

carcasses are more likely to be usurped by other burying beetles (Trumbo, 1991), which will kill the entire resident brood (Trumbo, 1990). Completing reproduction as soon as possible is particularly important on large carcasses because the risk of usurpation is not constant; in *N. orbicollis* the risk of takeovers decreases after five days (Robertson, 1993), possibly because depletion of the carcass due to larvae feeding makes it more difficult for free-flying beetles to detect. Moreover, the brood is less likely to be killed by a vertebrate scavenging the carcass if reproduction is completed sooner (Trumbo, 1992). Here, we addressed the following four questions: (1) Are the assumptions of the hurry-up hypothesis met in this system? If so, females could shorten the time to offspring independence by commencing oviposition sooner and there would be a trade-off between commencing oviposition sooner and laying the eggs more synchronously. (2) Do females adjust egg laying in response to variation in environmental conditions? We predicted that females breeding on decomposed or larger carcasses would shorten the time until offspring independence by commencing oviposition sooner, and that they would lay their eggs more asynchronously. (3) Is breeding success influenced by females commencing oviposition sooner and by patterns of egg laying? We predicted that starting to lay sooner would be beneficial and that asynchrony would be detrimental in terms of the size, number or survival of larvae (4) Do females compensate for the fitness costs of asymmetric sibling competition? If so, we predicted that females would lay larger eggs towards the end of the laying sequence.

METHODS

Study animals

The beetles used in this study were from an outbred laboratory population maintained at the University of Edinburgh. Beetles were housed individually in clear plastic boxes (124 mm x 82 mm x 22 mm). They were kept at $20 \pm 2^\circ\text{C}$ (mean \pm range) under

constant light and were fed small pieces of organic beef twice a week. The beetles were sexually mature and of prime reproductive age (18–26 days post-eclosion) at the start of the experiments.

Experimental procedures

The aim of the carcass decomposition experiment was to determine whether females attempt to shorten the time until offspring independence when the carcass is at a more advanced stage of decomposition at the start of the breeding attempt and whether this is associated with greater levels of hatching asynchrony. We provided females with either a fresh mouse carcass that had been thawed immediately before it was provided to the beetles ($n = 36$) or a decomposed carcass that had been left in the breeding box for 10 days before it was provided to the beetles ($n = 35$). The carcasses used in this experiment weighed 23.32–29.50 g (mean 25.57 g) when initially thawed. We initially set up pairs on 42 fresh and 59 decomposed carcasses but excluded all pairs where the eggs did not hatch (fresh carcasses: $n = 3$; decomposed carcasses: $n = 21$) and where there were technical problems (fresh carcasses: $n = 3$; decomposed carcasses: $n = 3$). The aim of the carcass size experiment was to determine whether females attempt to complete reproduction sooner on larger carcasses. We allowed beetles to breed on a range of carcasses ($n = 82$) from 4–27 g, which is within the range of vertebrate carcasses utilised by beetles in the wild (range: 1–37 g; Müller et al. 1990). We initially set up 92 pairs but excluded 1 pair that failed to lay eggs and 9 pairs that failed to hatch larvae.

For both experiments, we paired unrelated virgin males and females and placed them in a clear breeding box (170 mm x 120 mm x 60 mm) containing <1cm of moist compost. We supplied each pair with a previously frozen mouse carcass (supplied from Livefoods Direct Ltd, Sheffield, UK). Eggs are visible at the bottom of the breeding box

and can be seen on images obtained by placing the boxes on flat-bed scanners
(Canon Canoscan 9000F Mark II, Canon Inc., Tokyo, Japan) (Ford and Smiseth, 2016).

In the small amount of soil used, the visible number of eggs is very similar to the actual
clutch size (Monteith et al. 2012). We scanned the breeding boxes every hour using

170 Vuescan professional edition software (Hamrick Software, Sunny Isles Beach, FL, USA)

until the eggs hatched. In accordance with previous studies, we defined a clutch as
comprised of all eggs laid before the first larva hatched (Müller, 1987; Steiger, 2013).

From the scanned images, we counted the number of new eggs laid each hour to
determine the laying spread (the time between the first and last egg being laid) and the

175 clutch size (the number of eggs laid before the first egg hatched, Müller et al. 1990).

We excluded clutches where all eggs failed to hatch because females will continue to
lay eggs if larvae do not arrive at the carcass, resulting in aberrant laying patterns

(Müller, 1987). We also calculated a laying skew index reflecting the extent to which
laying is skewed towards the earlier part of the laying period, using the formula $\sum((t_i -$

180 $t_m)/t_m)p_i$, where p_i is the proportion of the total clutch laid each hour, t_i is the time
interval starting from the initiation of oviposition and t_m is the middle of the laying period

(Smiseth et al. 2008). We recorded the number of days since pairing until the larvae
dispersed from the carcass and counted the number of larvae dispersing from each

brood. At the time of dispersal, we also weighed the entire brood mass and calculated

185 the average larval mass by dividing the brood mass by the number of larvae in the
brood.

We measured egg size in the carcass decomposition experiment to determine
whether females compensated for the consequences of asymmetric sibling competition
caused by asynchronous hatching by increasing egg size across the laying sequence.

190 Using ImageJ (Abramoff et al. 2004), we split the clutch approximately into thirds and
measured the length and width of 3 eggs from the first third (first eggs), 3 eggs from the
second third (middle eggs), and 3 eggs from the last third of the clutch (last eggs). We

only measured eggs that were lying flat against the bottom of the box. If there were several suitable eggs on a single scan, we randomly chose which ones to measure.

195 Three broods were excluded for the middle eggs because there were no suitable eggs to measure that had not already been measured as either first or last eggs due to small clutch sizes. Eggs were measured from the second image on which they were present as they appear to shrink during the first hour after being laid. Each egg was measured three times and the mean length and width for each egg was used to calculate a
200 prolate spheroid volume (V) using the equation $V = (1/6)\pi w^2 L$, where w is the width and L the length of the egg (Berrigan 1991). We did not measure eggs in the carcass size experiment because laying asynchrony did not differ with carcass size once the greater clutch sizes on larger carcasses were taken into account and therefore we did not expect that there would be sufficient asymmetric sibling competition to elicit a
205 response from females attempting to compensate.

Statistical analyses

We carried out the statistical analyses in R (R Core Team, 2014). We constructed generalised linear models. Graphical model validation showed that the residuals of the
210 model were normally distributed and homoscedastic, that there was no over dispersion and that the model was not biased by unduly influential observations. Variance inflation factors confirmed that there was not excessive collinearity of the variables. We carried out model refinement through backwards stepwise deletion to determine the significance of each term comparing otherwise identical models either including or
215 excluding the term of interest using likelihood ratio tests. We then removed the least significant term and repeated the process until only significant terms remained. We used correlation tests (Pearson's correlation test, or Kendall's Tau correlation where the data did not fit a normal distribution) to investigate whether a shorter delay until

laying after females encountered the carcass was associated with earlier larval
220 dispersal or greater laying asynchrony.

We initially produced a model for each response variable containing only
treatment to determine whether there was an effect of carcass decomposition or
carcass size. We then produced full models containing covariates to investigate
whether any difference between treatments was solely due to variation between
225 treatments of other correlated variables. All analyses for the carcass decomposition
experiment contained treatment (fresh or decomposed carcass) and all analyses for
the carcass size experiment contained treatment (carcass size), as these were the
focus of the experimental manipulation (Tables 1 and 2). The models for laying skew
and laying spread included clutch size because it may take longer to lay larger clutches.

230 We also included the delay until the first egg was laid in the models for laying skew
because starting to lay sooner after encountering the carcass might affect laying
patterns. In the models for the time until dispersal, we included laying spread because
larvae in synchronous broods disperse sooner after arriving at the carcass than those
in asynchronous broods (Ford and Smiseth 2016), and clutch size because larger
235 clutches may use up the resource more quickly and therefore disperse sooner. The
models for the absolute number of larvae dispersing and the proportion of eggs
producing larvae that survived to dispersal included laying spread and the delay until
the first egg was laid to test for a cost of asynchronous laying or starting to lay sooner
after encountering the carcass. We also included clutch size in the models for the
240 number of larvae dispersing because the number of dispersing larvae is limited by the
number of eggs. We included clutch size in the models for the proportion of eggs
producing larvae that survived to dispersal because females usually lay a greater
number of eggs than the number of larvae the carcass can support so in large clutches
a smaller proportion of the clutch may go on to produce dispersing larvae even if the
245 viability of the eggs does not differ. The models for the mean larval mass at dispersal

(excluding broods for which larvae hatched but no larvae survived to dispersal) included laying spread and the delay until the first egg was laid to test for a cost of asynchronous hatching or starting to lay sooner, and the number of larvae dispersing in case there was a trade-off between number and size of larvae (Smiseth et al. 2014).

250 To determine whether egg size varied with laying order in the carcass decomposition experiment, we constructed a general linear mixed model using the restricted maximum likelihood method including laying spread, delay until the first egg was laid, stage (first, middle or last eggs) and treatment (fresh or decomposed carcasses) and the interaction between stage and treatment as fixed effects and brood
255 as a random effect in the lme4 package (Bates et al. 2015). We carried out stepwise model reduction using likelihood ratio tests.

RESULTS

Are the assumptions of the hurry-up hypothesis met?

260 We found that larvae dispersed from the carcass earlier when females commenced oviposition sooner in the carcass decomposition experiment (Pearson's correlation $t_{61} = 3.99$, $P = 0.0002$; Figure 1A). However, there was no evidence that larvae dispersed from the carcass earlier when females commenced oviposition sooner in the carcass size experiment (Pearson's correlation $t_{67} = 0.055$, $P = 0.956$; Figure 1B). Thus, we
265 found some evidence that females can shorten the time to offspring independence by commencing oviposition sooner, but this response was conditional upon the specific environmental conditions of the two experiments.

As expected if starting to lay sooner after encountering the carcass leads to greater laying asynchrony, we found that laying spread was greater when females
270 commenced egg laying earlier in the carcass size experiment (Pearson's correlation $t_{80} = -2.27$, $P = 0.026$; Figure 1D) and for females breeding on fresh carcasses in the carcass decomposition experiment (Kendall's Tau correlation $z = -2.15$, $P = 0.032$)

However, there was no evidence for such a trade-off for females breeding on decomposed carcasses ($z = -0.17$, $P = 0.863$; Figure 1C). Thus, we found some evidence for a trade-off between starting to lay earlier and laying synchronously, but only when females bred on fresh carcasses.

Do females adjust egg laying in response to environmental conditions?

Contrary to what we predicted, there was no evidence that females commenced oviposition sooner on decomposed carcasses compared to fresh ones ($F_{1,69} = 3.04$, $P = 0.086$; Figure 2A) or as carcass size increased ($F_{1,80} = 2.19$, $P = 0.142$; Figure 2B). As a consequence, there was no difference in either the time until the first larvae hatched ($F_{1,69} = 0.45$, $P = 0.505$) or the time until larval dispersal between females breeding on decomposed and fresh carcasses ($F_{1,62} = 0.40$, $P = 0.528$). Likewise, there was no difference in the time until hatching started between females breeding on different sized carcasses ($F_{1,79} = 1.84$, $P = 0.179$). We found that larval dispersal was delayed as a function of increasing carcass size ($F_{1,67} = 8.66$, $P = 0.004$).

In contrast to what we predicted, we found that laying spread was less pronounced on decomposed carcasses than on fresh carcasses ($F_{1,69} = 26.54$, $P < 0.0001$; Figure 2C). This difference was independent of clutch size as it persisted when we controlled for the effect of clutch size ($F_{1,68} = 13.49$, $P = 0.00047$). Thus, females were able to lay a given clutch size more synchronously on decomposed carcasses. There was a significant increase in laying spread with carcass size ($F_{1,80} = 6.22$, $P = 0.015$; Figure 2D). However, this effect was not statistically significant when we controlled for the effects of clutch size ($F_{1,79} = 0.28$, $P = 0.597$). We included clutch size in the model because females laid a greater number of eggs on larger carcasses (Pearson's correlation: $t = 6.13$, $P < 0.0001$) and females took longer to lay larger clutches ($F_{1,79} = 8.34$, $P = 0.005$) on a given carcass size. Thus, the increase in laying

spread on larger carcasses was likely to be solely due to the concurrent increase in clutch sizes. The laying skew index was negative for more than 90% of broods in both experiments, reflecting that the majority of the eggs were laid towards the start of the laying period. The laying skew index did not differ between females breeding on fresh and decomposed carcasses ($F_{1,69} = 0.03$, $P = 0.870$), and was not influenced by carcass size ($F_{1,80} = 3.38$, $P = 0.070$).

Does ovipositing sooner and laying asynchronously influence breeding success?

There was no evidence that starting to lay sooner had any effects on breeding success as the time until females started laying had no effect on either the number of dispersing larvae (decomposition experiment $X^2_{1,68} = 0.05$, $P = 0.816$; carcass mass experiment $X^2_{1,79} = 2.89$, $P = 0.089$) or the mass of these larvae (carcass decomposition experiment $F_{1,60} = 0.0038$, $P = 0.951$; carcass size experiment $F_{1,65} = 0.91$, $P = 0.345$).

Not only was the proportion of eggs hatching into larvae that reached independence lower on decomposed carcasses than fresh carcasses ($F_{1,69} = 8.92$, $P = 0.004$), there was also a detrimental effect of laying asynchrony on offspring survival with fewer offspring surviving in clutches with a greater laying spread ($F_{1,68} = 6.07$, $P = 0.016$).

However, there was no effect of laying asynchrony on offspring survival in the carcass size experiment ($F_{1,79} = 2.14$, $P = 0.148$). Laying spread had no effect on the absolute number of larvae dispersing (carcass decomposition experiment $X^2_{1,68} = 1.413$, $P = 0.235$; carcass size experiment $X^2_{1,79} = 0.17$, $P = 0.682$), the time until dispersal (carcass decomposition experiment $F_{1,59} = 0.07$, $P = 0.798$; carcass size experiment $F_{1,66} = 1.03$, $P = 0.314$) or larval mass (carcass decomposition experiment $F_{1,60} = 1.63$, $P = 0.207$; carcass size experiment $F_{1,65} = 1.32$, $P = 0.255$).

Do females lay larger eggs towards the end of the laying sequence?

325 Egg volume varied across the laying sequence ($X^2_2 = 86.24$, $P < 0.0001$), reflecting that last-laid eggs were smaller than first-laid eggs for females breeding on both decomposed (Wilcoxon matched pairs test: $V = 602$, $P < 0.0001$) and fresh carcasses ($V = 615$, $P < 0.0001$). Furthermore, egg volume was greater for females breeding on fresh carcasses than on decomposed ones ($X^2_1 = 5.60$, $P = 0.018$) and there was a
 330 significant effect of the interaction between carcass decomposition and laying order on egg volume ($X^2_2 = 8.00$, $P = 0.018$). This interaction effect reflected that there was a greater change in egg volume across the laying order for females breeding on fresh carcasses than for females breeding on decomposed carcasses. There was no evidence that egg volume was associated with either the time until females
 335 commenced oviposition ($X^2_1 = 0.01$, $P = 0.945$) or laying spread ($X^2_1 = 1.34$, $P = 0.250$).

DISCUSSION

Here, we report the results of the first test of the hurry-up hypothesis in a non-avian species. This hypothesis was originally proposed as an explanation for asynchronous
 340 hatching in birds but would also apply to non-avian species, such as *N. vespilloides*, provided that the following assumptions are met: (1) starting to lay sooner should shorten the time to offspring independence, and (2) starting to lay sooner should lead to greater laying asynchrony. Our study provides some evidence that both assumptions are met in *N. vespilloides*. Firstly, females were able to shorten the time to offspring
 345 independence as larvae dispersed earlier when females commenced oviposition sooner after encountering the carcass (though this was the case only in the carcass decomposition experiment). Secondly, there was evidence of a trade-off between commencing oviposition sooner and laying the eggs more synchronously (though this was not the case for females breeding on decomposed carcasses). Therefore, our
 350 results show that, as suggested by the hurry-up hypothesis, female burying beetles could shorten the time until offspring independence by starting to lay sooner after

encountering the carcass, and that this in turn could lead to greater levels of laying asynchrony as a by-product. In addition to the two assumptions mentioned above, the following three predictions must also be supported for the hurry-up hypothesis to be accepted: (1) females should commence oviposition sooner when environmental conditions provide an incentive for accelerated offspring independence (such as breeding on decomposed and larger carcasses), (2) commencing oviposition sooner should have positive effects on breeding success, and (3) increased levels of hatching asynchrony should be detrimental for offspring fitness. Although multiple tests are required to test the hurry-up hypothesis, it is highly unlikely that it would be accepted due to Type 1 error given that this would require false positives for both assumptions as well as for all three predictions. As detailed below, we did not find sufficient evidence in support of the predictions of the hurry-up hypothesis in *N. vespilloides*. Furthermore, we urge caution when interpreting results for the covariates included in our models due to the potential for Type 1 errors associated with multiple testing.

In contrast to what we predicted, we found that females started ovipositing at a similar time after encountering the carcass regardless of whether they were breeding on decomposed or fresh carcasses. Consequently, there was no difference in the timing of larval dispersal between females breeding on decomposed carcasses and fresh carcasses. The latter result contrasts with a previous study on the same species, which found that dispersal occurred later on decomposed carcasses than on fresh carcasses (Rozen et al. 2008). The different results of this previous study may reflect differences in methodology as it used experimental foster broods that were completely synchronous and smaller than our natural broods (Rozen et al. 2008), while we allowed females to rear their own broods without interference. We also found that females started laying at the same time after encountering a carcass regardless of its size. This result contrasts with previous work in the closely related *N. orbicollis*, which showed that larger carcasses took longer to bury and prepare and that oviposition therefore

was delayed on these carcasses (Scott and Gladstein 1993; Scott and Panaitof 2004).

380 This discrepancy may be due to the differences in carcass preparation and burial
between the two species, reflecting that *N. orbicollis* need to bury the carcass fully
beneath the soil while *N. vespilloides* does not (Pukowski 1933). We found that larvae
dispersed later on larger carcasses, possibly reflecting that larvae on smaller
carcasses exhausted the resource more quickly. This is consistent with previous work
385 on *N. orbicollis*, which found that larvae on larger carcasses took longer to develop
leading to later dispersal (Trumbo 1991; Scott and Gladstein 1993). Although there
may be an incentive to accelerate offspring independence on larger carcasses due the
increased risk of usurpation by other beetles and increased difficulty controlling
microbial growth, larger carcasses also represent a more valuable resource that can
390 sustain a greater number of larvae and larger larvae than smaller carcasses. These
factors could interact in a complex manner to determine the optimal laying behaviour
depending on the size of the carcass being used. In summary, our results provide no
evidence that females shortened the time until the offspring reached independence on
decomposed and larger carcasses by commencing oviposition sooner on these
395 carcasses.

We found that there was a greater laying spread on larger carcasses, but only
because females laid a greater number of eggs on these carcasses and females took
longer to complete larger clutches. This finding suggests that females adjust clutch size
rather than hatching pattern in response to variation in carcass size and that any effect
400 on laying spread is a by-product of the number of eggs laid. We found that females
breeding on decomposed carcasses laid a given clutch size more synchronously than
those breeding on fresh carcasses, suggesting that the former may attempt to lay as
synchronously as possible without incurring too great a cost through a decrease in egg
size or the female's body condition. We found some evidence of a cost of
405 asynchronous laying in that fewer offspring survived from the egg stage until dispersal

in more asynchronous broods in the carcass decomposition experiment. Previous work suggests that larvae hatching from the last-laid eggs in asynchronous clutches suffer increased mortality (Smiseth et al. 2008; Takata et al. 2014; Ford and Smiseth 2016). When females breed on decomposed carcasses, late-laid eggs may be at a greater disadvantage because the poor value of the carcass as a nutritional resource and reduced egg survival caused by microbes (Jacobs et al. 2014). Thus, under these circumstances, it may be highly advantageous for females to minimise laying spread. In contrast, it may be less advantageous for females to minimise laying spread when breeding on fresh carcasses, where moderate hatching asynchrony has a negligible effect on size or number of offspring. We found no evidence of a cost of asynchronous hatching for any aspect of offspring fitness in the carcass size experiment. The detrimental effects of hatching asynchrony may be less pronounced on larger carcasses (Müller et al. 1990) because there are sufficient resources for later-hatched larvae to survive even if they are considerably smaller than their siblings. This may explain why females breeding on large carcasses do not appear to attempt to minimise laying spread in large clutches because moderate hatching asynchrony is not detrimental under these circumstances.

If females attempted to compensate for competitive asymmetries due to asynchronous hatching, we might expect an increase in egg size across the laying sequence, as reported for some birds (Schrantz 1943; Kendeigh et al. 1956; Holcombe 1969; Howe 1976, 1978; Bryant 1978; Hillström 1999). Although egg size did vary with laying order, we found that egg volume decreased from first to last eggs for both fresh and decomposed carcasses, which is in the opposite direction to what we predicted. The decrease in egg size across the laying order would further disadvantage the last larvae to hatch because smaller eggs have lower survival as shown in *N. quadripunctatus* (Takata et al. 2015). The last offspring to hatch are out-competed by their siblings that hatched earlier and have already grown to a larger size (Smiseth et al.

2007). However, due to the lesser laying spread on decomposed carcasses, competitive asymmetries would be reduced relative to fresh carcasses because the earlier larvae will have had less of a head start. Laying the clutch as synchronously as possible when breeding on a decomposed carcass may therefore reduce competitive asymmetries to a greater extent than adjusting egg size. Thus, females may favour completion of laying as soon as possible over increasing egg volume across the clutch as a means to compensate for competitive asymmetries due to asynchronous hatching.

Overall, our results are not consistent with the hurry-up hypothesis given that females do not attempt to accelerate offspring independence under conditions where this would be favourable, such as when breeding on large carcasses or carcasses that have already started to decompose. Given that females breeding on decomposed carcasses laid more synchronously than those breeding on fresh carcasses, our results also show that females detect cues about the state of the carcass and adjust their laying spread accordingly. Our results also show that there is a survival cost to offspring in asynchronous clutches in the carcass decomposition experiment whilst there are no detectable benefits of asynchronous laying in any treatment. It is therefore unclear why hatching asynchrony occurs given that females are capable of laying more synchronously. Asynchronous hatching has evolved independently in many different taxa including insects, reptiles, fish and birds. However, no consensus has yet been reached on how asynchronous hatching evolves in any system. Several hypotheses have been proposed to explain the occurrence of asynchronous hatching in birds, many of which are based on constraints on the onset of incubation or adaptive incubation patterns. These hypotheses do not apply to *N. vespilloides* because it does not incubate its eggs. Previous work on *N. vespilloides* has found no evidence for the peak load reduction (Smiseth and Morgan 2009) and sexual conflict hypotheses (Ford and Smiseth 2016). Thus, the only remaining hypotheses are the brood reduction (Lack 1947; 1954) and insurance hypotheses (Stinson 1979). It seems unlikely that the

original version of the brood reduction hypothesis (Lack 1947; 1954) would apply to *N. vespilloides* because brood reduction in this species occurs through filial cannibalism rather than sibling competition (Bartlett 1987). Nevertheless, late-hatched larvae grow less well and beg more (Smiseth et al. 2008), and are at a higher risk of being the victim of filial cannibalism (Andrews and Smiseth 2013; Takata et al. 2013). Thus, a modified version of this hypothesis may apply to burying beetles if asynchronous hatching somehow facilitates brood reduction through filial cannibalism. The insurance hypothesis (Stinson 1979) suggests asynchronous hatching serves as insurance against mortality of core offspring. This hypothesis may apply to burying beetles because many eggs fail to hatch and females may produce additional eggs as insurance (Bartlett 1987). The hypothesis proposes that late-hatched marginal offspring normally only survive if core offspring fail to hatch or die soon after hatching. The brood reduction hypothesis and insurance hypothesis may interact because, if all core offspring hatch, asynchronous hatching may provide an efficient mechanism for brood reduction (Forbes 1990). Further studies on asynchronous hatching in our system and other non-avian systems should therefore focus on these hypotheses.

FUNDING

This work was supported by a Natural Environment Research Council studentship to LEF (NE/L501566/1).

We thank Matthieu Paquet for assisting with the experimental work. We also thank members of the beetle lab in Edinburgh, Maarit Mäenpää, Matthieu Paquet, Paco Garcia-Gonzalez, Lars Hillström, and one anonymous reviewer for helpful comments on the manuscript. We also thank Daniel Rozen for providing beetles from the Netherlands, and the City of Edinburgh Council Ranger Service for permission to

collect beetles in Edinburgh. This study was funded by a Natural Environment Research Council studentship to LEF (NE/L501566/1).

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Ford and Smiseth (2017).

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Figure 1

610 Effect of the delay until females commenced oviposition after encountering the carcass
on the number of days until larval dispersal in the carcass decomposition experiment
(A) and carcass size experiment (B) and on the laying spread (the number of hours
between the first and last egg being laid) in the carcass decomposition experiment (C)
and carcass size experiment (D). In (A) and (C) open circles represent values for
615 females breeding on fresh carcasses and filled circles represent values for females
breeding on decomposed carcasses.

Figure 2

Effect of carcass decomposition (A) and carcass size (B) on the delay until females
620 commenced oviposition after encountering the carcass and effect of carcass
decomposition (C) and carcass size (D) on the laying spread (the number of hours
between the first and last egg being laid). Error bars show standard errors.

Table 1

Outputs of models investigating female laying behaviour in response to carcass decomposition (treatment) and the consequences for the offspring. Significant effects are in bold.

Response	Model terms	Test statistic	p-value	Parameter estimate, SE	95% confidence intervals for parameter estimates	Error family
Time until first egg	treatment	$F_{1,69}=3.04$	0.0857	-0.015, 0.008	-0.030, 0.0005	Gamma
Time until hatching	treatment	$F_{1,69}=0.45$	0.505	-0.0003, 0.0004	-0.030, 0.0005	Inverse gaussian
Time until dispersal	treatment	$F_{1,61}=0.40$	0.528	0.139, 0.219	-0.290, 0.567	Gaussian
	clutch size	$F_{1,60}=5.92$	0.018	-0.029, 0.012	-0.053, -0.006	
	laying spread	$F_{1,59}=0.07$	0.798	0.003, 0.011	-0.019, 0.025	
Laying spread	treatment	$F_{1,69}=26.54$	<0.0001	-0.0009, 0.0002	-0.001, -0.0006	Inverse gaussian
	clutch size	$F_{1,68}=2.73$	0.103	<-0.0001, <0.0001	<-0.0001, <0.0001	
Laying skew	treatment	$F_{1,69}=0.03$	0.870	-0.007, 0.040	-0.085, 0.072	Gaussian
	clutch size	$F_{1,68}=0.04$	0.837	-0.0005, 0.002	-0.005, 0.004	
	delay until first egg	$F_{1,68}=1.39$	0.242	-0.004, 0.004	-0.011, 0.003	
Proportion of eggs	treatment	$F_{1,69}=8.92$	0.004	0.209, 0.070	0.072, 0.346	Gaussian
surviving to	laying spread	$F_{1,68}=6.07$	0.016	-0.009, 0.004	-0.016, -0.002	

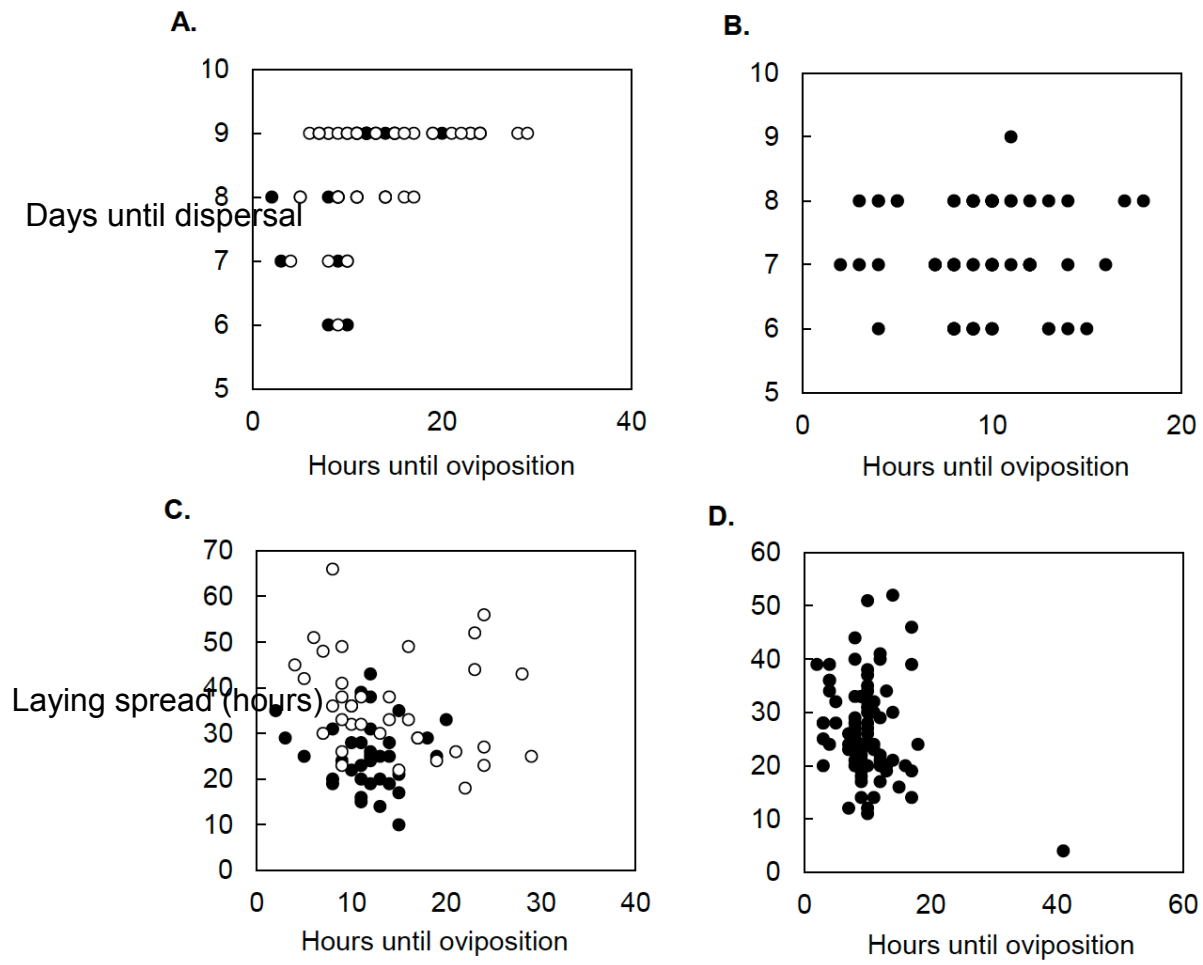
dispersal	clutch size	$F_{1,67}=2.23$	0.140	-0.006, 0.004	-0.014, 0.002	
	delay until first egg	$F_{1,67}=1.97$	0.165	0.009, 0.006	-0.003, 0.021	
Number of larvae at	treatment	$X^2_{1,69}=17.64$	<0.0001	0.936, 0.220	0.504, 1.368	Negative binomial
dispersal	clutch size	$X^2_{1,68}=0.72$	0.397	0.010, 0.013	-0.013, 0.034	
	laying spread	$X^2_{1,68}=1.41$	0.235	-0.013, 0.012	-0.035, 0.009	
	delay until first egg	$X^2_{1,68}=0.05$	0.816	0.004, 0.020	-0.032, 0.042	
Mean larval mass	treatment	$F_{1,61}=99.78$	<0.0001	0.078, 0.008	0.063, 0.094	Gaussian
(excluding zeroes)	no. of larvae	$F_{1,60}=0.93$	0.339	-0.0003, 0.0003	-0.001, 0.0003	
	laying spread	$F_{1,60}=1.63$	0.207	0.001, 0.0004	-0.0003, 0.001	
	delay until first egg	$F_{1,60}=0.004$	0.951	<-0.0001, 0.0007	-0.001, 0.001	
Mean larval mass	treatment	$F_{1,69}=99.55$	<0.0001	0.103, 0.010	0.083, 0.124	Gaussian
(including zeroes)	no. of larvae	$F_{1,68}=1.21$	0.275	0.001, 0.0005	-0.0004, 0.001	
	laying spread	$F_{1,68}=0.06$	0.804	-0.0001, 0.0006	-0.001, 0.001	
	delay until first egg	$F_{1,68}=0.55$	0.462	-0.0007, 0.001	-0.003, 0.001	

Table 2

Outputs of models investigating female laying behaviour in response to carcass size and the consequences for the offspring. Significant effects are in bold.

Response	Model terms	Test statistic	<i>p</i> -value	Parameter estimate, SE	95% confidence intervals for parameter estimates	Error family
Time until first egg	carcass mass	$F_{1,80}=2.19$	0.142	0.001, 0.0007	-0.0004, 0.002	Gamma
Time until hatching	carcass mass	$F_{1,79}=1.84$	0.179	<-0.0001,<0.0001	<-0.0001,<0.0001	Inverse gaussian
Time until dispersal	carcass mass	$F_{1,67}=8.66$	0.004	0.040, 0.014	0.013,0.067	Gaussian
	clutch size	$F_{1,66}=0.68$	0.411	0.011, 0.013	-0.014,0.036	
	laying spread	$F_{1,66}=1.03$	0.314	0.012, 0.011	-0.011, 0.034	
Laying spread	carcass mass	$F_{1,80}=6.22$	0.015	<0.0001,<0.0001	<-0.0001,<-0.0001	Inverse gaussian
	clutch size	$F_{1,79}=8.34$	0.005	<-0.0001,<0.0001	<-0.0001,<-0.0001	
Laying skew	carcass mass	$F_{1,80}=3.38$	0.070	-0.005, 0.003	-0.010, 0.0003	Gaussian
	clutch size	$F_{1,79}=1.52$	0.221	-0.003, 0.003	-0.008, 0.002	
	delay until first egg	$F_{1,79}=0.17$	0.678	0.002, 0.004	-0.006, 0.010	
Proportion of eggs	carcass mass	$F_{1,80}=0.86$	0.356	0.004, 0.004	-0.004, 0.012	Gaussian
surviving to	clutch size	$F_{1,79}=0.007$	0.932	0.0003, 0.004	-0.008, 0.008	
dispersal	laying spread	$F_{1,79}=2.14$	0.148	-0.005, 0.004	-0.012, 0.002	

	delay until first egg	$F_{1,79}=1.43$	0.235	-0.007, 0.006	-0.020, 0.005	
Number of larvae at	carcass mass	$\chi^2_{1,80}=3.94$	0.047	0.031, 0.015	0.0004, 0.062	Negative binomial
dispersal	clutch size	$\chi^2_{1,79}=3.81$	0.051	0.025, 0.014	-0.0001, 0.050	
	laying spread	$\chi^2_{1,79}=0.17$	0.682	-0.005, 0.012	-0.029, 0.020	
	delay until first egg	$\chi^2_{1,79}=2.89$	0.089	-0.051, 0.023	-0.108, 0.008	
Mean larval mass	carcass mass	$F_{1,67}=40.05$	<0.0001	0.004, 0.0006	0.003, 0.005	Gaussian
(excluding zeroes)	no. of larvae	$F_{1,66}=22.48$	<0.0001	-0.002, 0.0004	-0.002, -0.001	
	laying spread	$F_{1,65}=1.32$	0.255	-0.0005, 0.0004	-0.001, 0.0003	
	delay until first egg	$F_{1,65}=0.91$	0.345	0.001, 0.001	-0.001, 0.003	
Mean larval mass	carcass mass	$F_{1,80}=15.53$	0.0002	0.004, 0.001	0.002, 0.006	Gaussian
(including zeroes)	no. of larvae	$F_{1,79}=9.55$	0.003	0.002, 0.0007	0.0008, 0.003	
	laying spread	$F_{1,78}=0.03$	0.863	0.0002, 0.0009	-0.002, 0.002	
	delay until first egg	$F_{1,78}=0.30$	0.588	-0.0008, 0.002	-0.004, 0.002	

[Figure 1]

[Figure 2]